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Comparative fibre digestion

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Terrestrial ecosystems are marked by the ubiquity of plant material – 'primary producers' which do not live off other organic material. This plant material is available to 'primary consumers' – herbivores – of an enormous variety of body sizes, ranging from small insects to sauropod dinosaurs. It is the often large size of the primary consumers that truncates many trophic chains in terrestrial ecosystems: plant – gazelle – lion contains only two animal players; plant – elephant even contains only one. This contrasts with marine ecosystems, where the primary production is usually consumed by very small primary consumers, which are at the bottom of long trophic chains of predators of ever-increasing size. Large-bodied herbivory has only rarely evolved in marine ecosystems (very few fish, sea turtles, sirenians).

The comparison with marine environments highlights a feature terrestrial plants evolved in their struggle for access to light exposure – structural fibres that withstand gravity. Because in terrestrial, gravity-dominated ecosystems plant size is a competitive factor in the struggle for resources, the availability of plant material is particularly high in these systems; yet, this material predominantly consists of structural fibres. Structural fibres not only support the plant, but they also make it less vulnerable to predation: hardly any multicellular organisms produce enzymes that can digest structural fibres. One of the reasons why there are so few specialized large marine herbivores may be that in the marine environment, plant material is rarely available in the large portions necessary to support large-bodied organisms.

The only organisms that can digest structural plant fibre on a large scale are microbial – mainly bacteria, archea, but also fungi and protozoa. Many of the fibre-digesting microbes are basically anaerobic. Anaerobic conditions usually occur in sediment or detritus, and the first terrestrial food chains are believed to have consisted of detritus – detritivores – insectivores – higher-order predators (Sues & Reisz 1998). The emergence of herbivory was a 'late' step in many different animal lines, and was possible by what is maybe one of the most comprehensive examples of symbiosis in our planet's history: larger-bodied animals offer their microbial endosymbionts an anaerobic, protected, and relatively stable environment with a more or less guaranteed nutrient influx (often including a nitrogen recycling), and the anaerobic microbes offer their hosts the metabolites they produce during the digestion of structural fibres. Some hosts have evolved

further mechanisms to not only make use of the metabolites of their endosymbionts, but also digest surplus symbiont biomass itself – a symbiotic relationship termed 'farming' (Karasov & Martínez del Rio 2007). Limited evidence suggests that nematodes might have a similar symbiotic function for some herbivore hosts (Pryor & Bjorndal 2005b, a; O'Grady & Dearing 2006); why this relationship appears to be limited to ectotherms (amphibians and reptiles) so far is an intriguing question.

A predominant characteristic of herbivory is the similarity of the microbial fauna found in herbivore hosts. Among mammals, for example, phylogenetically very distant hosts share a characteristic microbial fauna as a convergent adaptation (Ley et al. 2008). Important variations are expected in sensitivity to temperature (between the faunas of poikilothermic and homoiothermic hosts). Microbial digestion of fibre is relatively uniform across herbivorous host-microbe-symbioses, and results in the production of short-chain fatty acids (SCFA) by the microbes, which are absorbed by the host (Stevens & Hume 1998). In other anaerobic fermenting systems (such as detritus, or sewage plants), the SCFA are further degraded into methane, CO_2 and H_2O.

A major difference in the fauna of various herbivores may be the kind and proportion hydrogen-removing microbes. Hydrogen accumulates as NADH during microbial fermentation and must be removed by 'hydrogen sinks' for the system to remain productive; this can either be done by methanogenesis (conversion of CO_2 and H_2 into CH_4 and H_2O) or acetogenesis (conversion of H_2, H and HCO_3 into acetate and H_2O). While current evidence suggests that all terrestrial vertebrate herbivores produce methane to some degree, functional ruminants are exceptional in this respect with their particularly high methane output (Franz et al. 2011b). Because SCFA are the relevant gain for the host, methanogenes that use SCFA as a substrate, as they occur in detritus or sewage plants, are not a relevant component of the symbiotic microbial population (Van Soest 1994).

From a background of work with domestic production animals, where increasing food conversion efficiency and reducing waste accumulation is the aim of solution-oriented research, the question whether microbial systems more efficient at fibre fermentation existed in the past – such as in herbivorous dinosaurs - is understandable. From an evolutionary point of view, given the inconceivably long time during which microbes adapted to fibre fermentation, it is difficult to fathom that possible increases in fibre digestion efficiency have not yet evolved.

Convergence among herbivores cannot only be found in their microbial symbionts, but also in morphological and physiological adaptations to the ingestion of fibrous food, and its digestion by the microbial symbionts. For example, herbivores usually have more digestive tract tissue than carnivores, and the proportion of body mass allocated to the gastrointestinal contents appears to be remarkably constant across different vertebrate clades, possibly indicating a general, intrinsic bauplan constraint. On the one hand, detailed differences exist between herbivore species in

the morphological design of sections of the gastrointestinal tract dedicated to hosting symbiotic microbes. On the other hand, general design principles, such as taeniae and haustrae, occur in various morphologies (Langer & Takács 2004). There are two basic layouts of the herbivore digestive tract. Depending on the site of the 'fermentation chamber', herbivores are grouped into foregut and hindgut fermenters (Stevens & Hume 1998). Differences between these digestion types are related to the sequence of microbial and auto-enzymatic digestion; however, it should be noted that most 'foregut fermenters' also have fermentative digestion occurring in their hindgut, and that so far, there is little indication that metabolic or endogenous faecal losses vary systematically between the groups. The adaptations for herbivory in terms of head morphology, bite force, and structure of the digestive tract have been nicely demonstrated in the case of a rapid evolutionary divergence in a 36 year-experimental introduction of an omnivorous lizard to an island environment in which it had to adapt to a higher degree of herbivory (Herrel et al. 2008).

Digestive efficiency is mainly determined by food quality, by ingesta retention time, and by ingesta particle size (Hume 2005). General differences between plant food categories will be reflected in morphophysiological adaptations of different herbivore feeding types (Hummel et al. 2006). Retention time and ingesta particle size reduction can actually compensate for each other, because larger particles usually require a longer time for complete digestion. The acquisition of energy, however, is not merely dependent on digestive efficiency, but also on absolute food intake. Yet an increase in food intake will reduce the time available for a careful selection of high quality forage, will – due to the higher input in the system – decrease ingesta retention time, and may also compromise the efficiency of particle size reduction. This conflict between food intake and factors influencing digestive efficiency represents the typical 'herbivore dilemma'. Animals differ in the extent by which an increase in food intake will affect the parameters that influence digestive efficiency (Clauss et al. 2007). The trade-off between food intake and digestive efficiency means that animals rarely optimize intake or digestive efficiency, but seek to maximize net energy gain by a compromise between these two factors (Hume 2005). In this respect, animals can be classified along a gradient from a low intake/high efficiency to a high intake/low efficiency strategy; in particular, foregut fermentation appears to limit animals to the former strategy unless it is coupled with rumination (Clauss et al. 2010). Among mammals, two not closely related herbivores in an otherwise carnivorous order, the Giant panda (*Ailuropoda melanoleuca*) and the Lesser panda (*Ailurus fulgens*), show a remarkable convergence in their nearly exclusive use of bamboo forage; in doing so, they represent the most extreme examples of a high intake/low efficiency strategy, in which plant fibre is hardly fermented (Dierenfeld et al. 1982).

Two major characteristics of the host organisms are generally considered crucial for digestive physiology: the level of metabolism, and body size. Animals of a higher metabolism need to maintain net energy gains at higher rates than animals with a low metabolism. Homoiothermic

animals, such as birds and mammals, are therefore characterised by efficient particle size reduction mechanisms (gizzard grinding; mastication) (Fritz et al. 2011); they achieve similar digestive efficiencies as poikilothermic animals such as reptiles, but at higher intake rates. A comparatively low metabolism is usually linked to a low intake/high efficiency strategy. However, the level of metabolism must have other effects on the digestive tract than just a restraining the level of food intake. At dry matter intakes of 30 g $kg^{-0.75}$ d^{-1} or below, at which low-metabolism mammals such as sloths or vombats achieve average fibre digestibilities, the digestive efficiency of ruminants or horses is seriously compromised (Doreau et al. 2003; Clauss et al. 2008), although the low intake is associated with long retention times and should therefore allow particularly high digestive efficiencies.

Effects of body size are most evident when comparing extremes. For example, due to the dramatic difference in the ratio of gut surface to gut volume between termites and cattle, the problem of maintaining anaerobic gut content is relevant in the termites, which therefore require particular oxygen sinks to maintain an evironment favourable for fibre digestion (Karasov & Martínez del Rio 2007). It is generally thought that small animals consume higher quality food because they can feed more selectively, and that they have shorter ingesta retention times, which prevents them from using high-fibre forage efficiently. While such differences appear evident when comparing mammals and reptiles across a body size range of four to five magnitudes, empirical data does not suggest that retention times vary distinctively with body mass above 1 kg (Franz et al. 2011a); additionally, digestive efficiency does not seem to drop necessarily with small body size (Justice & Smith 1992; Pérez-Barberìa et al. 2004). Because several disadvantages may also be associated with fibre digestion in larger herbivores (Clauss & Hummel 2005), common concepts that interpret large body size as an adaptation to high-fibre herbivory should be evaluated with caution. Among mammals, differences in body mass may be responsible for two general different strategies to cope with variability in diet quality. The 'anticipatory response' implies that herbivores increase intake on high quality forage, building up body stores, and reduce intake on lower quality forage; this strategy is only feasible above a certain body size threshold that allows body store accretion. The reason for the reduction in intake on lower quality forage still need to be elucidated, and may lie in costs, in terms of metabolic/endogenous losses, associated with the digestion of such forage. Limited evidence suggests that small mammal herbivores may use the 'instantaneous response', wich implies that they respond to lower quality forage by an increase in intake. These animals usually practice coprophagy/cecotrophy, a strategy that minimises metabolic/endogenous losses (Meyer et al. 2010).

Herbivore guts have been analysed as according to principles of chemical reactors (Jumars 2000), and further insight into the processing of plant fibre by animals is considered crucial for the development of more efficient bioreactors (Bayané & Guiot 2011). Apart from details on the

composition of the microbial fauna, nutrient supply, endogenous losses and links to the host metabolism, understanding the relevance of digesta washing is an important area of future research. Comparisons of particle and solute ('fluid') retention in the digestive tract of mammalian herbivores suggests that while the retention of particulate digesta per se is rather independent of the morphology of the digestive tract, the movement of digestive fluids in relation to the particles varies with the morphophysiological design of the digestive tract (Müller et al. 2011). Adapting insights on digesta washing and microbial harvest by increased fluid throughput to bioreactors might be one possible route to technical progress.

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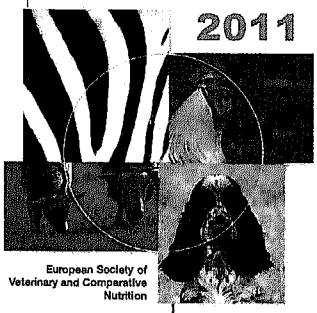

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